LIGHT INTENSITY AND MELANOPHORE RESPONSE IN THE MINNOW, ERICYMBA BUCCATA COPE

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Although every investigator of chromatic response in animals is well aware that light intensity has a profound effect upon the coloration of animals, this knowledge is at most qualitative and is in general restricted to the effects of the presence or absence of light. Fishes become pale in darkness as a rule while in light the response is governed by the color of the background. Considering that many animals with responsive pigmentary systems are normally accustomed to live at relatively low intensities of light, it was believed of significant value to investigate the behavior of fish from this viewpoint, and perhaps to derive simultaneously more information in regard to the sensitivity of the photoreceptors and the manner in which they function to produce adaptive color changes. In this latter regard Keeble and Gamble (1904), Bauer (1905), Sumner (1911), von Frisch (1911), Sumner and Keys (1929), Pearson (1930), and Sumner (1933) have concluded that the color of the animal is determined by the ratio of incident and reflected light striking the eye of the animal. Should this statement hold true without modification, then it would follow that for a given background which is characterized by always reflecting a given percentage of the light striking it, the animal would remain the same shade at all effective light intensities and there would exist a sharp critical point in intensity of light at which a fish upon a black background would become pale as the light was decreased. Whether or not this is the actual state of affairs is tested in the following experiment.

I. Uniform Black Background and Varying Light Intensity

Material and Methods

In the experiment herein described the silver-mouthed minnow, *Ericymba buccata* Cope, was used exclusively. This fish is from five to eight centimeters in length and is found most abundantly in streams with sand bottoms in the region about Urbana, Illinois, (Thompson and Hunt, 1930). The fish used were always freshly caught, none

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being used after they had been in the laboratory tanks for more than a week. Furthermore, all the data were obtained from fish caught in a given region and within a period of less than two winter months, thus insuring fish that were quite uniformly pigmented. Because of the rapidity of color change in this species no method was devised whereby more than a single light intensity could be used in testing the quantitative response in any individual fish. As a result, the data included here are those of a population and hence characterized by considerable variation.

All the experiments were carried out in an experimental dark-room. The light sources used in obtaining the different intensities were a 200 watt tungsten lamp, a 75 watt daylight Mazda lamp, and a 25 watt tungsten lamp with a daylight filter. For the lower intensities the last lamp was enclosed in a light-proof container possessing an iris diaphragm over the single aperture. In addition, approximately neutral light filters (exposed photographic plates) were used. The measurement of the light intensity was made with a potassium photoelectric cell with maximum sensitivity in the blue end of the visible spectrum. This cell was constructed by Professor J. Kunz. In nearly every instance the light source was 125 centimeters directly above the 8 inch, flat-black-coated crystallizing dish in which the experimental fish were placed.

In order to test the effect of a given light intensity upon the response of the melanophores, two or three minnows were placed in the crystallizing dish containing three centimeters of water. The crystallizing dish was coated with flat-black paint because it was determined that upon a background of this nature the fish would become dark in color in the ordinary light intensities of the laboratory and would become pale in total darkness. Thus the actual intensity at which the fish would entirely cease to respond to the color of the background could be learned. At the end of two to three hours in the experimental situation, during which time the water in which the fish were kept was constantly aerated with compressed air and an aerator block, the fish were removed and immersed in boiling water for a minute or two. Then a piece of the integument from a given area of the fish was dissected off and mounted in glycerine. A Spencer camera lucida and a celluloid rule served in measuring the diameters of 30 to 80 melanin masses. The average was taken as an index of the degree of dispersion of the pigment in the fish as a whole. In order to ascertain that two hours was sufficiently long for the pigment masses to have reached an equilibrium point of dispersion within the melanophores for the light intensity and background in question, some of the fish were taken from a black background in light and others from a white background in light at the beginning of the experiment and thus the equilibrium points were reached from both sides. Furthermore, at the intensities of the ordinary daylight of the laboratory the color-change was very rapid, requiring only five or ten minutes to pass from one extreme to the other. Research is now in progress to determine to what extent the rates of color change are influenced by intensity.

Results

During the course of the experimentation 75 minnows were tested. These were roughly distributed among the seven light intensities in

TABLE I

Average diameters of melanin masses in fish kept upon a black background under measured light intensities. Pigment mass diameters are given in micra and light intensity in foot candles.

Light intensity						
.000005	.000053	.000625	.0125	.25	1.75	23.75
55.3	65.9	78.8	78.6	80.5	86.1	88.5
52.5	48.4	68.3	76.9	78.5	84.4	82.0
40.5	43.7	63.4	74.0	76.3	83.4	80.3
40.4	41.6	58.3	72.5	64.3	81.4	80.2
36.6	38.2	56.4	68.6	54.0	80.5	79.8
33.9	39.3	55.0	67.6	74.5	77.1	68.6
	36.3	51.9	59.6	73.6	77.0	66.7
	34.3	51.1	63.5	72.5	76.6	
	34.0	44.0	54.3	69.1	75.3	
	40.7	41.9	53.5	59.7	74.7	
	41.4	38.9	51.3	57.5	64.3	
		34.0	49.3	54.6		
			46.9			
			46.3			
			45.6			
			36.6			
Mean 43.1	43.4	53.4	59.2	67.9	78.3	78.0

proportion to the variability exhibited in the data. Table I is a summary of the results.

The averages for a number of fish have been calculated for each light intensity. The values for individual fish are shown diagrammatically in Fig. 1, plotted against the logarithm of the light intensity. These data strongly suggest that the relationship is most probably one of a direct proportionality over the complete range of dispersion of pigment mechanically possible in the melanophore of this fish. In

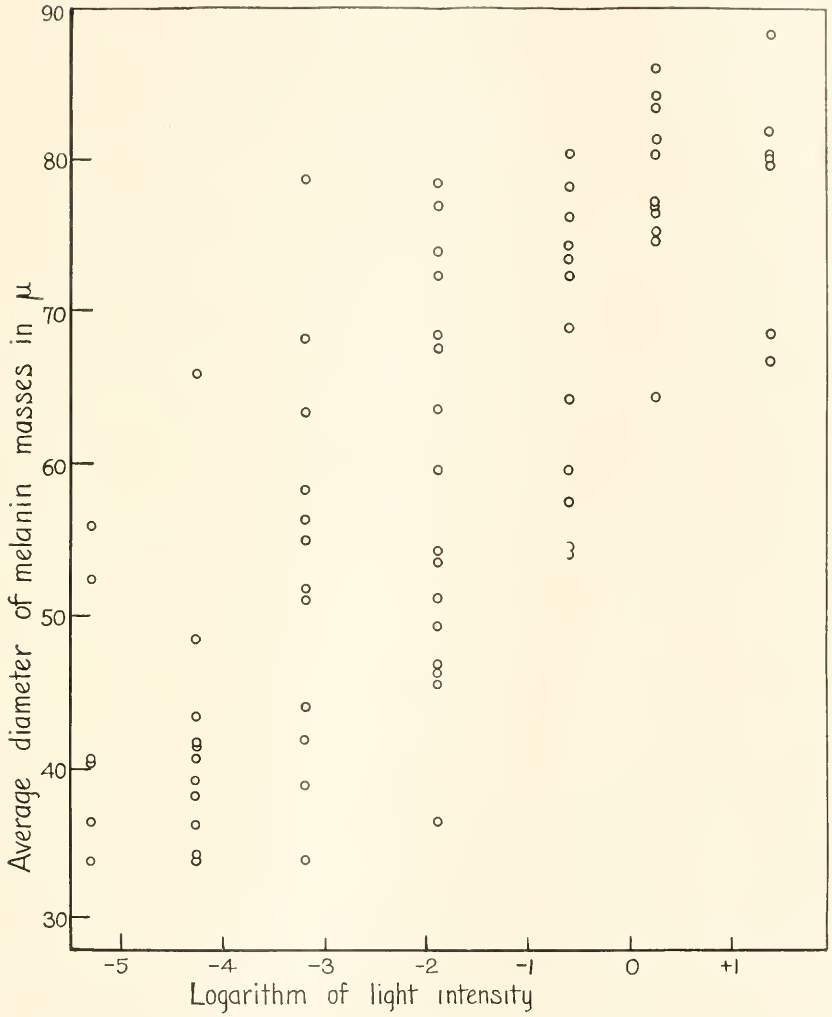

FIG. 1. Diagram showing the relationship between the logarithm of light intensity and the degree of melanin dispersion in the melanophores of *Ericymba buccata*. Each dot indicates the value for a single fish.

other words, the limits of this simple relationship are determined by the diameters of completely concentrated and fully dispersed pigment masses.

II. Uniform Light Source with Different Shades of Gray Backgrounds

Material and Methods

A second type of experiment was performed using the same material and methods as in the first, except that here the light was kept constant at 1.75 foot candles, the minimum intensity at which complete dispersion of melanin could be obtained in response to a black background. Six backgrounds were used, the black one of the previous experiment, a white one, and four of intermediate shades of gray. The latter five were obtained by placing a glass crystallizing dish upon paper and cloth of the appropriate shades. The relative brightnesses of the direct light at the level of the background and the light reflected from the background were measured with a Macbeth illuminometer equipped with a brightness-determining device consisting of a translucent white plate. The values obtained serve best as comparative ones. The value of the ratio, $\frac{\text{direct light}}{\text{reflected light}}$, obtained for the white background was 2.54; for the gray backgrounds, 6.60, 12.4, 35.4, and 140.; and for the black one, 201.

TABLE II

Average diameters of melanin masses in fish kept upon black, white, and gray backgrounds in an incident light intensity of 1.75 foot candles. The ratio indicates the $\frac{\text{incident intensity}}{\text{reflected intensity}}$. Pigment mass diameter is given in micra.

Background ratio					
2.54	6.60	12.4	35.4	140	201
37.2	38.2	35.6	56.0	75.7	86.1
31.6	39.2	35.0	45.3	73.6	84.4
35.7	36.2	40.0	42.7	70.7	83.4
37.9			40.9	68.0	81.4
40.3			40.7	63.0	80.5
32.3			41.4	57.1	77.1
			46.4	55.7	77.0
			74.5	77.8	76.6
			59.5	74.8	75.3
			37.3		74.7
			38.2		64.3
			46.7		
			48.6		
Mean 35.8	37.9	36.9	47.5	68.6	78.3

Results

The average diameters of the melanin masses in 45 fish kept upon these above-described backgrounds are recorded in Table II. The values for the black background have been taken from Part I of this paper. These results plotted as a dot diagram in Fig. 2 indicate that

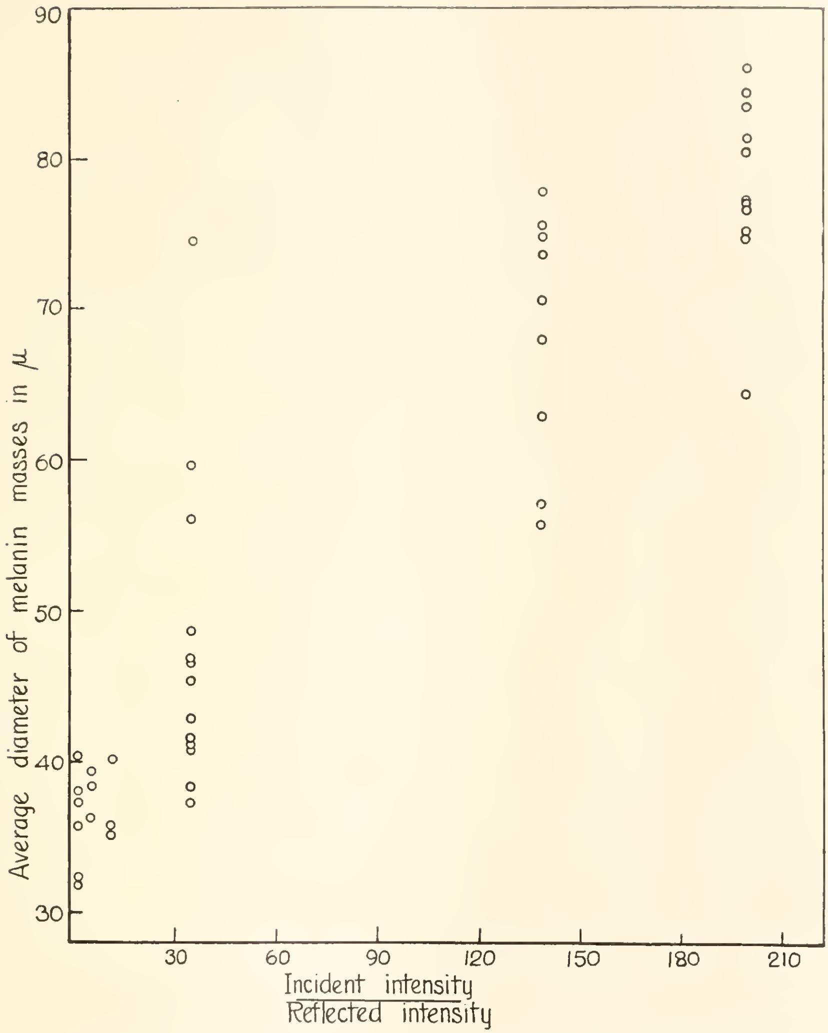

FIG. 2. Diagram showing the relationship between the ratio, $\frac{\text{incident light}}{\text{reflected light}}$, and the degree of melanin dispersion in the minnow, *Ericymba buccata*. Each dot indicates the value for a single fish.

for a given light intensity the average diameter of the pigment within the melanophore is a direct function of the ratio of incident to reflected light.

General Considerations

The ratio of incident to reflected light is thus seen to be inadequate to account completely for the degree of melanophore dispersion even when the intensity is considerably above the value of zero. Total intensity has a marked and significant effect. Duspiva (1931) found that light intensity had a very great effect upon the coloration of larvæ of *Perca fluviatilis*, *Salmo salvelinus*, and some other fishes. Background was without effect upon these forms. Koller (1934), however, reported that for larval *Coregonus* the background was the principal stimulus for melanophore activity while the light intensity had no influence until complete darkness was attained. These two papers are characteristic of the extremes in the literature regarding the effect of light intensity upon melanophores in fishes. The present research does not pretend to give a complete answer to this problem of long standing. Rather, it merely suggests that both forces are quite definitely influential in altering the coloration of fishes, but that the degree of overlapping of the two or the dominance of a single one determines the differences between individual species and even the same species at different developmental periods.

It is a well-known fact to fishermen of the Illinois River that when the water is laden with silt and consequently permits light to penetrate only a very short distance in any quantity, the fishes taken are pale in color, whereas in clear water the fishes are invariably dark in shade. If fishes swimming freely at some distance from the bottom in clear water can be figured as being upon the equivalent of a black background since practically no light is reflected from below, then the silt in the more turbid waters can be conceived of as having effect through reduction of incident light and also augmentation of the reflected light entering the eyes of the fishes.

In closing, I wish to acknowledge my indebtedness to Dr. David H. Thompson of the Illinois Natural History Survey and to Professor J. Kunz of the Physics Department, University of Illinois, for generously supplying me with helpful suggestions and material during this investigation.

Summary

1. A quantitative method of determining the influence of the environment upon the melanophores of small fishes is described.

2. The degree of dispersion of the melanin in the melanophores of the silver-mouthed minnow, *Ericymba buccata*, is within certain limits determined by the total light intensity as well as by the shade of the background.

3. Upon a constant black background between the intensities of light, .000053 and 1.75 foot candles, the average diameter of pigment masses is directly proportional to the logarithm of the light intensity.

4. At an intensity of less than .000053 foot candles the fish are at their maximum degree of paleness in spite of a black background.

5. At 1.75 foot candles illumination the fish becomes maximally dark upon a black background, and the average diameter of melanin masses appears to vary in a directly proportional fashion with the ratio, $\frac{\text{incident light}}{\text{reflected light}}$, which reaches the eyes of the fish.

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